

SIGNIFICANCE OF POLAR DINOSAURS IN GONDWANA

THOMAS H. RICH

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Polar dinosaurs have been found at four localities in the southern hemisphere and eight in the northern. Three groups of dinosaurs, neoceratopsians, ornithomimosaur and oviraptorosaurs, previously known only from the Late Cretaceous of the northern hemisphere were present in the Early Cretaceous polar dinosaur fauna of southeastern Australia. Labyrinthodont amphibians were also present, but do not occur in the same deposits as crocodylians. Enlarged optic lobes of the hypsilophodontid *Leaellynasaura*, suggesting enhanced ability to see under low light conditions, is the only adaptation to a polar environment yet recognised in a dinosaur. Polar dinosaurian taxa are not unique at the familial level, but belong to more widespread families. Polar dinosaurs probably lived under cold climates quite unlike those tolerated by modern reptiles. □ *Early Cretaceous, southeastern Australia, dinosaurs, labyrinthodonts, palaeoclimate.*

Thomas H. Rich, Museum of Victoria, P.O. Box 666E, Melbourne, Victoria, Australia; 5 April 1996.

Only one area within the palaeo-Antarctic Circle has produced dinosaurs — southeastern Australia (Aptian-Albian, early Cretaceous). Four more are known to have been close to the palaeo-Antarctic Circle — southeastern Queensland, Australia (early or middle Jurassic), Beardmore Glacier, Antarctica (early Jurassic), James Ross and Vega Islands, Antarctica (Campanian and Maastrichtian, late Cretaceous) and North Island, New Zealand (probably Maastrichtian, late Cretaceous). In the Northern Hemisphere, eight areas (late Jurassic? to late Cretaceous) are known to have produced dinosaurs within the palaeo-Arctic Circle (Fig. 1). Most of the polar dinosaur material from both hemispheres was acquired during the past twenty years and much of it remains to be described (Table 1).

Polar Gondwana may have served as both a refuge and birthplace for some dinosaur groups.

From the early or middle Jurassic of southeastern Queensland has come a partial skeleton of one of the earliest sauropods, *Rhoetosaurus brownii* Longman, 1927.

A single astragalus suggests that the well-known form *Allosaurus* may have persisted into the Aptian of southeastern Australia after having become extinct elsewhere at the end of the Jurassic.

On the basis of one or a few bones, the presence of three groups previously known in the late Cretaceous of the Northern Hemisphere has been suggested in the early Cretaceous of southeastern Australia. An ulna from the Aptian there bears an uncanny resemblance to that of the Maastrichtian protoceratopsian *Leptoceratops gracilis* from Alberta, Canada. This suggests that Polar

Gondwana may have been the place of origin for the neoceratopsians, for they are known nowhere else prior to the Late Cretaceous.

Ornithomimosaur are represented in the Albian of southeastern Australia by femora distinct enough to base a new genus and species, *Timimus hermani* Rich & Vickers-Rich, 1994. As yet undescribed ornithosaur vertebrae are known from both the same Albian site that produced femora from southeastern Australia as well as Aptian sites a few hundred kilometres to the east. This material suggests a presence for this group on the Gondwana continents prior to when ornithomimosaur are best known in the northern hemisphere, the late Cretaceous. However, the recent publication of *Shuvosaurus inexpectatus* Chatterjee, 1993 from the late Triassic of Texas, implies that ornithomimosaur have had a much longer history in the northern hemisphere than previously suspected. The late Jurassic *Elaphrosaurus bambergi* from Tendaguru, Tanzania, formerly regarded as an ornithomimosaur, has recently been allocated to the abelisaur (Holtz, 1994).

Oviraptorosaurs, previously represented exclusively in the late Cretaceous of the northern hemisphere, appear to have been present in the Albian of southeastern Australia based on a partial surangular and a vertebra (Currie, Vickers-Rich & Rich, 1996).

Associated with these dinosaurs is the most unexpected and best documented temporal range extension of a major tetrapod group. Two decades ago, labyrinthodont amphibians were thought to have become extinct at the end of the Triassic.

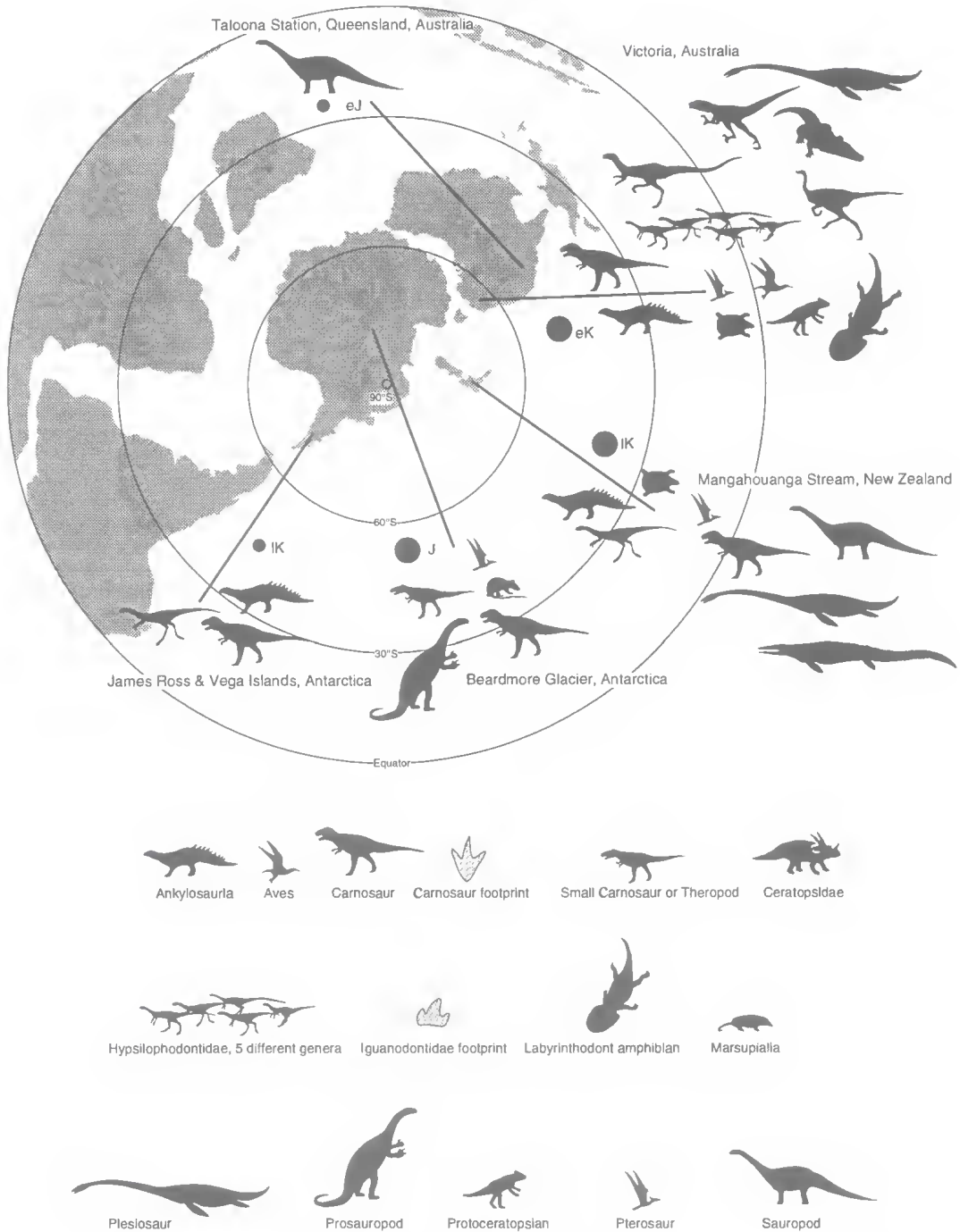


FIG. 1. Distribution of polar dinosaurs, Southern Hemisphere (this page) and Northern Hemisphere (facing page). Dinosaur sites in polar latitudes are not common, most having been discovered in the last 20 years. None are fully studied. The higher diversity in southeastern Australia is probably due to greater collecting effort and easier accessibility. When some of the other sites are more fully studied, they may provide similar diversity. Base map from Smith, Hurley & Briden (1981).

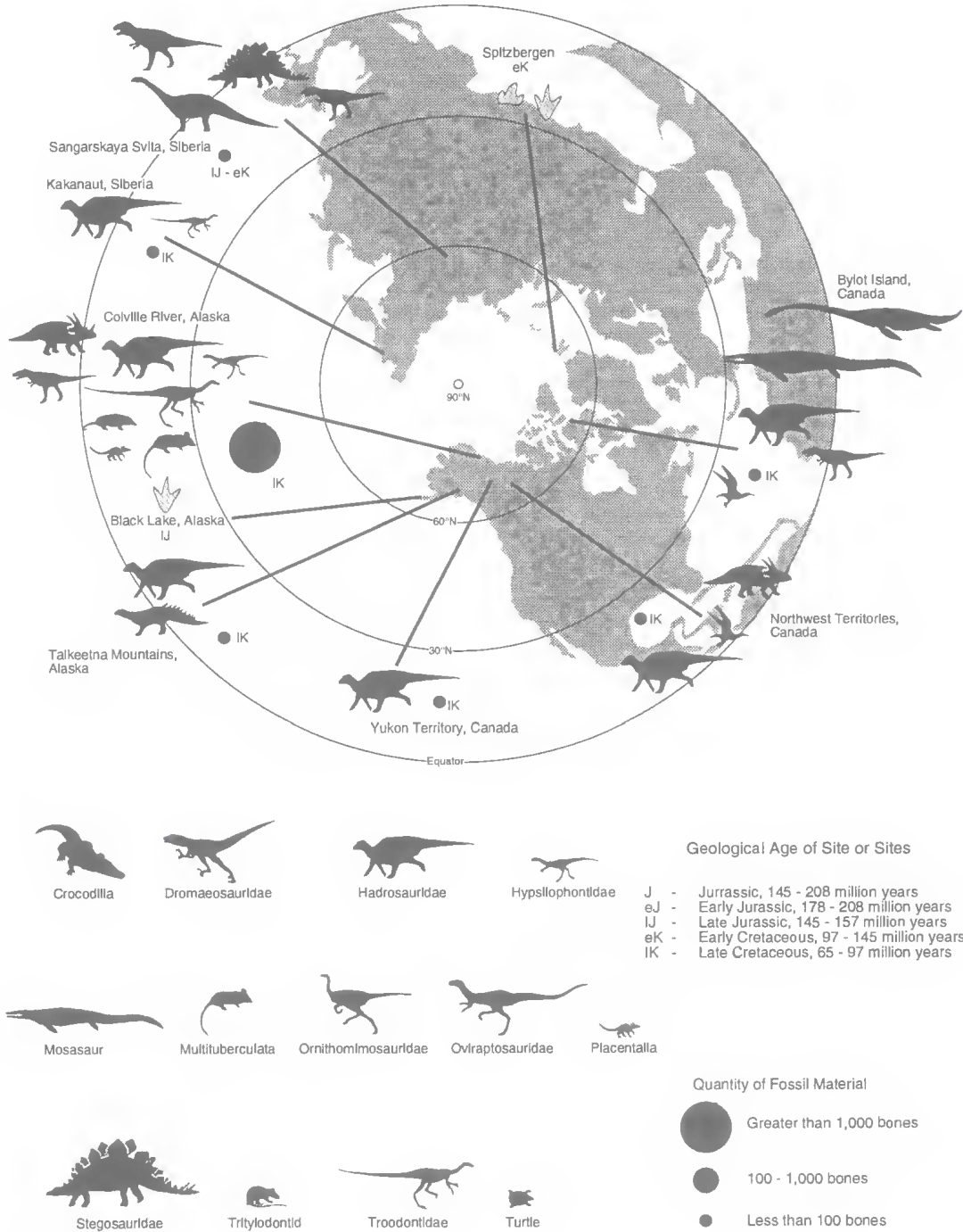


FIG. 1 (cont.).

Subsequent to that, they have been described from the early Jurassic of Australia (Warren & Hutchinson, 1983), middle Jurassic of China

(Dong, 1985) and late Jurassic of Mongolia (Shishkin, 1991). Nearly complete lower jaws with teeth, pectoral girdle elements, and ver-

tebrae form the basis for recognition of their presence in the Aptian of southeastern Australia (Warren, Kool, Cleeland, Rich & Rich, 1991; Warren, Rich & Vickers-Rich, in press).

Crocodylian-like in their overall morphology, the latest survivors of this once dominant group of amphibians may have found a final refuge in Aptian polar southeastern Australia because of a greater tolerance of cold, as is true of modern frogs and salamanders, than the crocodylians which appeared there subsequently in the Albian when conditions became warmer. There is no trace of an Albian labyrinthodont in the southeastern Australian deposits where crocodylians are represented by a few dermal scutes.

Among polar dinosaurs from either hemisphere, only one feature of one individual has yet been interpreted as an adaptation to life in a high latitude environment. This may reflect more the fact that very little is known about these animals and less published, than that they rarely displayed marked differences between themselves and their lower latitude contemporaries. The feature in question is the enlarged optic lobes of the brain that occurred on the holotype of the hypsilophodontid *Leaellynasaura amicagraphica* Rich & Rich, 1989 from the Aptian of southeastern Australia. Hypertrophy of this structure formed the basis for the suggestion that this animal had enhanced ability to see under the low light conditions that would have prevailed during the prolonged periods of continuous darkness each Winter.

Hypsilophodontid dinosaurs are generally a rare element in most dinosaur assemblages. Even where specimens are relatively common, as on the Isle of Wight, their taxonomic diversity is not great. Southeastern Australia is a marked exception to that generalisation. At least six species in five or six genera occur there; just over half the total dinosaurs recognised to date. Currie (pers. comm.) has suggested that hypsilophodontids may have been primarily an upland group at lower latitudes, hence their general rarity there, and are better represented in southeastern Australia because of its cooler conditions.

In this regard it may be noteworthy that the dinosaur known from the late Cretaceous of Vega Island is a hypsilophodontid or dryosaurid (Milner & Hooker, 1992) and that of the four found at Mangahouanga Stream, New Zealand, one is a probable dryosaurid, a family closely related to hypsilophodontids (Wiffen & Molnar, 1989). This explanation for the apparent preponderance of these groups at high latitude may well be true.

However, in the much more fossiliferous Liscomb Bonebed locality on the Colville River, Alaska, hypsilophodontids are all but unknown despite the extensive sieving programme carried out there (Clemens & Nelms, 1993; pers. obs.). The age of the site is Maastrichtian and by that time there may not have been the variety of hypsilophodontids there was earlier in the Cretaceous. But that does not explain why the one known to occur there is not more abundant.

Today, there are no avian or terrestrial mammalian families restricted to the polar regions. As far as the available record has been analysed, the same can be said of the polar dinosaurs as previously independently noted by Molnar & Wiffen (1994). Although new genera and species have been recognised among them, they all belong to families also known at lower latitudes.

However, given the fragmentary nature of much of the evidence for the existence of various groups, this could be an artefact. If one had a single tooth of a litoptern and that group was otherwise unknown, depending on the species, the most parsimonious familial identification might be Equidae. In that case one would be parsimonious but one would be wrong. The recent identification of protoceratopsians in the Aptian of Australia (Rich & Vickers-Rich, 1994) could be a parallel case. On the basis of a single bone, rather than propose an entirely new group of vertebrates which would share an uncanny resemblance in the form of the ulna to protoceratopsians but would in some other way be distinct from them, the specimen was allocated to this known taxon which extended its record not only to another continent but also backwards in time by at least 15 million years. At our present state of knowledge that is an identification which is quite plausible but could well eventually prove to be fundamentally in error.

The Gondwanan polar dinosaur localities that form groups of the same age are quite meagre in their total faunal lists, making comparisons quite preliminary. It is fortuitous, however, that in the broadest terms, they share a common facies. Both early Jurassic sites are flood plain deposits and the three late Cretaceous ones, nearshore marine. It may be of some note that the New Zealand late Cretaceous locality shares ankylosaurs and dryosaurids/hypsilophodontids with the two sites in the Antarctic Peninsula, the only two dinosaurs known to occur in the latter region.

There is no evidence such as tillites to suggest that continental ice sheets existed during the Mesozoic at high latitudes (Frakes, Francis &

TABLE 1. Gondwana Polar Dinosaur Localities.

<p>1, Mt Kirkpatrick, Beardmore Glacier area, Transantarctic Mountains, Antarctica, 165°E, 84°S <i>Rock unit.</i> Falla Formation (fluvatile) <i>Age.</i> Jurassic on stage-of-evolution of dinosaurs <i>Palaeolatitude.</i> 61°S (Smith, Hurley & Briden 1981) <i>Palaeoenvironment.</i> Foreland basin flood plain <i>Recent Reference.</i> Hammer & Hickerson (1994) <i>Fauna.</i> <i>Cryolophosaurus ellioti</i>, plesiomorphic allosaurid (Hammer, pers. comm. to Molnar 1995); Small theropod; Prosauropod; Tritylodontid; Pterosaur</p>	<p>Plesiosaur Pterosaur Aves Labyrinthodont: New genus and species (Warren et al., in press) Ceratodontidae: <i>Ceratodus avus</i>, <i>Ceratodus nargun</i>, <i>Ceratodus</i> sp., <i>Coccolepis woodwardi</i>, <i>Wadeichthys oxyops</i>, <i>Koonwarria manifrons</i>, <i>Leptolepis koonwarri</i></p>
<p>2, Australia, Southeastern Queensland, Taloona Station near Roma, 149°03±3'E, 26°05±3'S. <i>Rock unit.</i> Walloon Coal Measures (Injune Creek Group) <i>Age.</i> Early Jurassic [?Bajocian] <i>Palaeolatitude.</i> 65°S (Douglas & Williams 1982), 56°S (Smith, Hurley & Briden 1981) <i>Palaeoenvironment.</i> Intracratonic flood plain <i>Reference.</i> Longman (1927) <i>Fauna.</i> Sauropoda: <i>Rhoetosaurus brownei</i></p>	<p>4, Antarctica, Antarctic Peninsula, James Ross Island, 57.9°W, 63.9°S <i>Rock unit.</i> Santa Marta Formation (Marambio Group) <i>Age.</i> Campanian <i>Palaeolatitude.</i> 65°S (Scotese et al. 1988) <i>Palaeoenvironment.</i> Nearshore marine <i>Recent Reference.</i> Gasparini, Pereda-S. & Molnar (1996, this volume) <i>Fauna.</i> Nodosauridae</p>
<p>3, Victoria, Australia, numerous sites centred on 38°45'S, 143°30'E. (Otway Group) and 38°40'S, 145°40'E (Strzelecki Group) <i>Rock units.</i> Strzelecki and Otway Groups (fluvatile) <i>Age.</i> Strzelecki Group Aptian except Koonwarra locality which is Albian; Otway Group Albian <i>Palaeolatitude.</i> Strzelecki Group, 77.8°S; Otway Group, 66.8°S. Minimum estimates because of thermal overprinting between 75 & 100my BP (Whitelaw 1993). <i>Palaeoenvironment.</i> Rift valley flood plain <i>Recent Reference.</i> Rich & Vickers-Rich (1994) <i>Fauna.</i> Hypsilophodontidae: <i>Fulgurotherium australe</i>, <i>Leaellynasaura amicagraphica</i>, <i>Atlascopcosaurus loadsi</i>, Victorian hypsilophodontid Type 1, Victorian hypsilophodontid Type 2, Victorian hypsilophodontid Type 3</p>	<p>5, Antarctica, Antarctic Peninsula, James Ross Island, 57.9°W, 63.9°S <i>Rock unit.</i> Hidden Lake Formation <i>Age.</i> Coniacian-Santonian <i>Palaeolatitude.</i> 65°S (Scotese et al. 1988) <i>Palaeoenvironment.</i> Nearshore marine <i>Recent Reference.</i> Molnar, Angriman & Gasparini (1996, this volume) <i>Fauna.</i> Theropod</p>
<p>Ornithomimidae: <i>Timimus hermani</i> Ankylosauria, cf. <i>Minmi</i> Protoceratopsidae: Aff. <i>Leptoceratops</i> Oviraptorosaur? Carnosauria: <i>Allosaurus</i> sp. Testudines: <i>Chelycarapookus arcuatus</i> (testudines) Testudines: Cryptodira</p>	<p>6, Antarctica, Antarctic Peninsula, Vega Island, 57.5°W, 63.7°S <i>Rock unit.</i> Cape Lamb Member of the Lopez de Bertodano Formation <i>Age.</i> Late Campanian - early Maastrichtian <i>Palaeolatitude.</i> 65°S (Scotese et al. 1988) <i>Palaeoenvironment.</i> Near shore marine <i>Recent Reference.</i> Milner & Hooker (1992). <i>Fauna.</i> Hypsilophodontidae</p>
	<p>7, New Zealand, North Island, Mangahouanga Stream, 176°45'E, 39°S <i>Rock unit.</i> Maungataniwha Sandstone <i>Age.</i> Late Cretaceous, Campanian - Maastrichtian <i>Palaeolatitude.</i> 55°S (Scotese et al. 1988) <i>Palaeoenvironment.</i> Nearshore marine <i>Recent Reference.</i> Molnar & Wiffen (1994) <i>Fauna.</i> Dryosauridae, Theropod, Ankylosauria, Sauropoda, Testudines, Plesiosauroidea, Mosasauridae, Pterosauria</p>

Syktus, 1992). However, it has been inferred on the basis of the occurrence of dropstones as large as 3m across in finegrained marine sediments deposited during the late Jurassic and early Cretaceous that winter seasonal ice did form at high palaeolatitudes in both hemispheres (Frakes, Francis & Syktus, 1992).

In southeastern Australia, studies assessing the mean annual palaeotemperature have been carried out on the sediments producing the dinosaurs. Palaeobotanical evidence based on leaf margin and stomatal structure together with the overall composition of the flora have been taken to suggest a mean annual temperature of +10°C (Parrish et al., 1991) while an oxygen isotope estimate is -6°C (Gregory et al. 1989), the difference between Chicago and Point Barrow, Alaska, today. While the biological implications of these two estimates are quite different, they are concordant in that the palaeoclimate was far from tropical.

No matter what the palaeotemperature was, polar dinosaurs would had to have adapted to prolonged periods of annual darkness each Winter. There have been suggestions that in the geological past the earth's rotational axis might have been significantly closer to being oriented perpendicular to the plane of the ecliptic (e.g., Douglas & Williams, 1982). If this had occurred, the length of continuous darkness each Winter at high latitudes would have been reduced. However, the criticism of Laplace (1829) against the earth's obliquity having shifted more than a few degrees from its present orientation as it does over a period of about 41,000 years (one of the components of the Milankovitch cycle), has never been refuted.

Of all the polar dinosaur sites, that on the Colville River, Alaska (Fig. 1), has the greatest potential to yield a detailed picture about these animals. For more than 200km on the left bank of that river are beautifully exposed outcrops that range in age from Albian to Maastrichtian. Fossil bones have been found at many places along that river. By contrast, the potential of sites which are shown as having less than 100 bones is much more problematical.

The work on the polar dinosaurs of Gondwana is just beginning. Just how distinctive they were from their lower latitude contemporaries is all but unknown. The Falla Formation of Antarctica seems the most promising area at the moment in terms of future potential. Southeastern Australian outcrops are limited to just 4 square kilometres which have been thoroughly prospected. In

another four years, the major sites there may be worked out. Outcrops of the Wallon Coal Measures are rare in southeastern Queensland. In the Mangahouanga Stream locality of New Zealand the fossil vertebrates are recovered from loose boulders in the stream itself and dinosaur remains are quite rare. The Ross Island occurrences, like the New Zealand ones, are marine but unlike there, partial skeletons rather than isolated bones have been found. Although Ross Island is unlikely to produce major concentrations of dinosaur remains, with persistent prospecting over the large available area, it may be expected to continue to contribute significantly to our knowledge of Gondwana polar dinosaurs. Clearly, to find significantly more information about Gondwana polar dinosaurs outside the area of the Falla Formation, new areas need to be investigated such as the Cretaceous coalfields of New Zealand (Rich, 1975).

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